

12.0 POPULATION MODELS

12.1 Introduction

A tremendous amount of work on ecological models has been published in the last few decades, including a number of books on the subject, and a journal, *Ecological Modeling*. The focus here will be on models that may be useful in collecting and assessing field data on actual populations. These may range from quite simple equations to complicated computer programs. Almost any kind of analysis depends on a model of some sort. Many scientists use various statistical tests without stopping to consider that each such test depends on a formal model.

The simple linear regression model, $y = a + bx$, serves to assess one possible relationship between paired observations. Fitting a regression model is usually (but not necessarily) done with the least-squares technique. The fitting process depends on the assumption of a model (linear in this case). If least-squares is used in fitting, it brings in the further assumption that the x -values are known exactly, so that the minimizing process involved in fitting deals only with variability in the y -variable (independent variable). For linear regression, this amounts to minimizing the quantity:

$$S = \sum_i [y_i - (a + bx_i)]^2$$

with respect to the coefficients (parameters) a and b .

Going beyond the fitting process to do statistical tests of various kinds requires some further assumptions. For linear regression, the main such assumption is that the model is actually of the form:

$$y_i = \alpha + \beta x_i + e_i \quad (12.1)$$

where the e_i are randomly drawn from a normal distribution with mean zero and a constant variance, σ^2 . We thus have a sequence of events in using models. First one settles on the mathematical form of the model, then on the method of fitting, and finally methods of analysis are considered, i. e., finding out whether the parameters are "significant" and how important they are in the process being studied.

Many population models use time as the independent variable, so that the variation in fitting can reasonably be assumed to be associated solely (or mainly) with the dependent variable. Consequently, least-squares is often an appropriate fitting technique. Unfortunately, many of the models that seem to be useful in ecology are fairly complicated. Consequently, most of the usual statistical analysis techniques can only be validly applied in considering components of the model, and become very doubtful indeed if applied to model outcomes.

This makes the relatively new technique of bootstrapping appear very promising for modelling, as it can be applied to very complex systems. One such application appears in Chapter 11, where bootstrapping and the delta method were applied to a complex model, the Lotka-Leslie model. Because the model has to be solved iteratively, least-squares is no help. Efforts to deal with

the underlying model mathematically depend on the calculus of complex variables and thus become difficult for most biologists. Bootstrapping, however, is quite straightforward and gives results supported by realistic-seeming stochastic models of actual populations.

12.2 Curve-fitting models

A natural extension of the simple linear regression model is to fit more complex curves. Multiple regression offers a simple extension of the linear regression model (eq. 12.1), taking the form:

$$y_i = b_0 + b_1x_1 + b_2x_2 + \dots b_kx_k + e_i \quad (12.2)$$

where the x_i are several (k) independent variables. Fitting is again readily done by least-squares. Many texts now give the relevant equations in matrix form. Mathematically and computationally speaking, a large number of independent variables can be used, but this is where a lot of biologists get into serious trouble without realizing what they are doing. Many of the available statistical packages will not only fit multiple regressions with many independent variables, but they will also "decide" which of the variables are "statistically significant" via stepwise regression. If fits with the observed variables (x_1, x_2 , etc.) aren't satisfactory, one can try various transformations, e.g., x_1^2 , $\log x_2$, $1/x_3$, etc., looking for a good fit.

The problem with this approach is that it may be difficult to justify even the simplest multiple regression model for biological data. Very often we can be quite sure that linear models are not suitable for biological relationships. Hence experimenting with combinations of variables until one gets a good fit should only be used for predicting a future y -value and then *only* if the model can be proof-tested on an independent data set. Otherwise such predictions may be an exercise in self-delusion.

The most frequently used model in population studies is undoubtedly the exponential function:

$$y = ae^{bx} \quad (12.3)$$

where a and b are again parameters. Usually $a = N_0$, the initial population size, $y = N_t$, current population size, and $x = t$, time of observations. The exponential function is non-linear, i.e., the variables are not related by simple additions and multiplications as in eqs. (12.1) and (12.2).

There are two ways to fit eq. (12.3). One is by non-linear least-squares which requires a computer fitting routine, now found in most statistical packages. Using that approach assumes that the underlying model is:

$$y_i = ae^{bx_i} + e_i \quad (12.4)$$

i.e., that the error terms are additive. The alternative is to take natural logarithms of the y_i , giving the log-linear regression model:

$$\log_e y_i = \log_e a + bx_i \quad (12.5)$$

which is readily fitted by simple linear regression. To justify eq. (12.5), one needs to write the underlying model as:

$$y_i = ae^{bx_i} e_i \quad (12.6)$$

thus assuming that the errors are multiplicative. This appears to be the appropriate model for population data. If one fits an exponential model to a sequence of observations of a population changing at a constant rate, and then examines the deviations of observed points from the fitted curve:

$$\text{Deviations} = y_i - N_0 e^{rt_i} \quad (12.7)$$

it usually turns out that the deviations increase in magnitude with time. Deviations from the log-linear model tend to be independent of time, giving a reasonably constant "variance about regression", and thus conforming approximately to the simple linear regression model requirement of constant variance.

The log-transformed approach using simple linear regression (log-linear regression) is thus to be preferred. This disturbs some workers, who prefer to think in terms of the observed population size. An obvious answer to that complaint is just to present the data in terms of the original measurements, i.e., numbers or counts, rather than the logarithms of those data. Doing so may draw criticism from statisticians, who point out that "transforming back" can introduce bias in estimates. However, the overwhelmingly important result from a log-linear analysis of population trend data is ordinarily the slope, which estimates the rate of change, r , directly (and thus does not need to be transformed back in any case). The other parameter in a fitted equation (N_0) seldom gets much attention, regardless.

In many instances, the basic data may be counts, rather than actual population estimates, so it makes good sense to stay on the logarithmic scale and graph the fitted relationship as a straight line. An advantage, as mentioned above, is that deviations from the fitted regression line tend to be more uniform over time, supporting the notion that log-linear regression gives a useful estimate of the rate of change.

One may thus be led to suppose that it will be acceptable to go ahead and obtain confidence limits for r in the usual manner for linear regression, and this seems to be a rather common practice. Unfortunately, there is reason to doubt that such limits will provide the degree of "confidence" one would expect. In simple linear regression 95% confidence limits on the slope can be interpreted to mean essentially that if we repeat the process generating the observed data many times, then 95% of the resulting estimates of r should fall within the confidence limits obtained in the first place. Hence, it might be supposed that if it were possible to observe many populations growing under conditions identical to the one population studied, about 95% should show values of r within the calculated confidence limits.

The problem is that normal theory confidence limits are based on the assumption that the "errors", e_i , of eqs. (12.1) and (12.5) are randomly and *independently* drawn from a normal distribution. For population growth, this

would mean that each increment of growth would be determined independently of previous increments. However, real populations, like real organisms, do not grow that way. A chance fluctuation early in time influences future population size. Consequently, a population experiencing, by chance, slow growth initially may have a trajectory appreciably below that of a population that happens to "get a good start".

The consequences of this phenomenon appear quite surprising. Eberhardt and Simmons (1992) used stochastic models of population growth for several species of large mammals to study behavior of the confidence limits generated from log-linear regressions on such data. Their results were expressed in terms of "coverage" of calculated confidence limits. That is, confidence limits calculated for log-linear regressions on each of 1,000 runs of a given population model were examined to see whether they included the true rate of population change expected from the population parameters used.

If confidence limits from log-linear regression applied to population growth data behaved as for ordinary linear regression, the anticipated coverage would be 95%. In the simulations, it was about 60%. This raises doubts about confidence limits for the rate of growth determined from log-linear regression. In practice, of course, other factors influence the observed variability, including sampling errors of the measurements of population size and year-to-year fluctuations of the actual rate of growth associated with environmental conditions.

The simulations of Eberhardt and Simmons (1992) did show that an accurate estimate of the rate of change can be obtained from trend data, so that estimating a rate of change from trend data complements estimates from reproductive and survival data very nicely (Fig. 11.12). The main problem is one of how to make comparisons between estimates from the two sources. Some unpublished simulations indicate that coverage from bootstrapping confidence limits based on the Lotka-Leslie model is very close to the expected 95%, so that, if there are no biases in the survival and reproductive estimates used in generating the estimate of λ , the confidence limits from bootstrapping provide a useful tool for further analysis.

It should be noted that there is a theoretical answer to the problem of poor coverage of confidence limits from loglinear regression on population trend data, but one that is impractical for population studies. The approach is that taken in studies of growth of individual organisms, where the same problem exists. In that case, one simply observes growth rates for a number of individuals, and confidence limits for the mean growth rate are based on the rates for the individuals. However, it is seldom feasible to study a number of independent populations under the same conditions, so using "replications" isn't a useful solution.

One further outcome of the simulations of Eberhardt and Simmons (1992) is useful. This is that confidence limits on projections of given populations a few years into the future did give acceptable coverage. It is thus evident that trend data can give useful estimates of rates of change, and provide worthwhile confidence limits on short-term projections of population size. The implication then is that a record of trend data provides useful information on variability for the observed population trajectory, but not for

other trajectories that might arise from the underlying survival and reproductive rates.

Consequently, if we have estimates of rate of change from reproductive and survival data and from trend data, it appears worthwhile to ask whether the estimate from trend data can be considered to be one realization of the many possible population trajectories that might arise by chance from the observed reproductive and survival data. One approach is to do a t-test. A difficulty is that the variance of the trend data estimate can be expected to be different from that obtained from reproductive and survival data. This leads to what statisticians know as the Behrens-Fisher problem. An approach using bootstrapping has been suggested by Efron and Tibishirani (1993).

12.3 Some growth curves

A number of equations other than the exponential have been used to represent the growth of populations, usually for laboratory studies or in the case of introduction into new habitat or after substantial reductions in numbers. Most of the curves are "sigmoid" or S-shaped with the initial stage characterized by nearly exponential growth, followed by a gradual tapering-off towards a constant, or asymptotic level. The curves to be described here are all deterministic, that is, do not take into account chance or stochastic fluctuations in numbers. Stochastic versions are available for several of the curves, but the details are mathematically complex.

All of these curves are also applicable to the study of growth of individual organisms, and several were originally developed for that purpose. Thus we may take the dependent variable, y , as representing either population size or the weight of an individual or average weight of a group of individuals, all presumably being of the same age. Since the curves are all continuous in form, we are effectively supposing the population to be large enough that it doesn't matter whether we use a continuous or discrete representation. This is also implied by the use of a deterministic as opposed to a stochastic model.

Since there are a substantial number of growth curves available, one needs some criteria for choice in particular circumstances. This is a problem that is not resolved. Both the growth of populations and that of individual organisms are sufficiently complex and variable to prevent a solution on purely theoretical grounds, and the choice is often one of convenience for the needs of the moment. Although theoretical bases are available for most of the curves, discussion here will largely be limited to one simple criterion - the rate of change per unit of time. Thus for exponential growth the rate of change is a constant fraction of y , that is, for a small increment of time (Δt) the incremental change in y (Δy) is proportional to y :

$$\frac{\Delta y}{\Delta t} = ry$$

so that, for population growth, this can be described as the difference between births, b (or recruits) per head and loss rate (d), giving

$$\frac{\Delta y}{\Delta t} = by - dy = (b-d)y = ry$$

If a continuous variable is involved, the differential notation is normally used, i.e.,

$$\frac{dy}{dt} = ry$$

It may be more convenient to study a given set of data in terms of a relative rate of change,

$$\frac{dy}{ydt} = r$$

so that one examines the rate of change divided by the current size. In examining a given set of data, one might thus decide on a convenient (but short) time interval, Δt , and determine whether the corresponding changes, Δy , are nearly constant fractions of current size (y). Of course the assumption of exponential growth can be examined much more readily by simply taking logarithms (or plotting on "log-log" paper), but such a simple approach is not available for many of the other growth curves. Such curves can often be fitted by non-linear least-squares (available in a number of commercial computer "packages"). When these routines fail to converge (or give dubious results), it is worthwhile to start over with guesses as to the parameters. Often the first derivatives given below can be used to obtain such starting values.

The remainder of this section will be devoted to a listing of a number of growth curves, the first derivative (dy/dt) and a few remarks. Most of the curves can be written in several forms. Those used here are largely as given by Grosenbaugh (1965). An extensive set of models for analysis of fish growth and survivorship is available in Schnute and Richards (1990). All of the curves described here (excepting, of course, the exponential) have an upper asymptote (denoted by A) which is approached as t becomes very large. All but one are sigmoid, or S-shaped. The exception is sometimes known as the "monomolecular" curve, and has the equation:

$$y = A(1 - e^{-Bt}) \quad (12.8)$$

Replacing e^{-Bt} by the first two terms in the series expansion ($e^{-Bt} \doteq 1 - Bt$) gives an approximation for small values of t :

$$y \doteq Abt$$

which shows that the curve starts out as nearly a straight line. As t becomes large, y gradually approaches A , so we have something like an inverted J, or a curve that is concave downwards. The first derivative (rate of change) can be written as:

$$\frac{dy}{dt} = B(A - y) \quad (12.9)$$

Thus when y is small the rate of change is nearly constant, indicating a straight line as suggested above. As y increases the slope diminishes, and ultimately reaches zero at the asymptote. For a given set of data, an investigator could calculate Δy for some small fixed Δt and expect that a plot of Δy against y would yield approximately a straight line:

$$\Delta y \doteq BA - By$$

and thus suggest the applicability of equation (12.8) as a model. In this case, however, the general shape of the curve should also give a first indication as

to its suitability. This curve has been used to represent the upper portion of growth curves, by simply disregarding the early stages of growth. One way to do this is to write the curve as:

$$y = A(1 - e^{-Bt}) + C$$

so that when $t = 0$, $y = C$ where C is the first value to be considered. Eq. (12.8) is also often useful if one wishes to fit curves to reproductive data as shown in Fig. 11.4. Sometimes it is possible to fit eq.(11.8) directly with non-linear least-squares, but this approach often will fail due to the number of parameters that need to be estimated. This is especially true when there is little data on senescence, as usually is the case. One may then attempt to approximate the curve in sections. Eq. (12.8) represents the left-hand side of the curves (Fig. 11.4), except that a constant (c) appears in eq. (11.8). This constant effectively represents the age at which an appreciable amount of reproduction is first observed (e.g., age 4 in the fur seal data of Fig. 11.4). One can thus obtain a useful guess at c and take a as the reproductive rate observed for prime-age individuals, and then fit the left-hand portion of the curve by non-linear least-squares.

Equation (12.9) indicates that the rate of change depends on y (and the constants A and B) but not on t -- that is growth depends only on the size already achieved, and not on time. A curve that brings in a dependence on time also, is named after the mathematician Gauss, has the following form:

$$y = A(1 - e^{-bt^2}) \quad (12.10)$$

and has the first derivative:

$$\frac{dy}{dt} = 2bt(A - y) \quad (12.11)$$

so that we have the rate of change again decreasing in proportion to size of y (just as in equation (12.9)), but there is an opposite effect due to the value of t .

Equations (12.8) and (12.10) may also be written with another constant (C) as multiplier for the exponential term:

$$y = A(1 - Ce^{-bt})$$

$$y = A(1 - Ce^{-bt^2})$$

which provides more flexibility in fitting data, for which the price paid is less assurance that the particular curve considered is somehow unique or "appropriate". In neither case does C appear in the first derivative.

The logistic (Verhulst) curve has probably been more widely used than any of the others. The equation is:

$$y = \frac{A}{1 + Ce^{-Bt}} \quad (12.12)$$

and the derivative is:

$$\frac{dy}{dt} = y(A - y) \quad (12.13)$$

which shows again a dependence on the approach to the asymptote through $(A - y)$, but now modified by the value of y . A plot of $\Delta y / \Delta t$ against y will now give a curve (a quadratic or second degree curve):

$$\frac{\Delta y}{\Delta t} = By - \frac{B}{A} y^2$$

In fisheries management, an important concept is that of a stock-recruitment curve, which compares the number of recruits to a fishery with the existing stock. These curves can be considered as growth curves. Because recruitment is often an annual or generational event, the underlying equations can best be expressed as difference equations, rather than the differential equations as in the other growth curves described here. Two stock-recruitment curves have been widely used, one being the Beverton and Holt curve (Beverton and Holt 1957) and the second due to W.E. Ricker, who described both curves in detail in his 1975 book (Ricker 1975). It can be shown that the Beverton and Holt curve can be written as a difference equation form of the logistic curve [eq. (12.12)] and that the Ricker curve approaches the Beverton and Holt curve under limiting conditions (Eberhardt 1977c). The Ricker curve is nonetheless different from the logistic and is worth separate listing here, being conveniently written as:

$$N_{t+1} = AN_t e^{-BN_t}$$

where N_t is the population size at time t (often at generation t , as for Pacific salmon where distinct generations are observed) and A and B are parameters.

A rather more complicated curve with an evident similarity to the logistic is the Pearl-Reed curve:

$$y = \frac{A}{1 + Qe^{-(Rt + St^2 + Ct^3)}} \quad (12.14)$$

which has the derivative:

$$\frac{dy}{dt} = \frac{y}{A} (A - y)(R + 2St + 3Ct^2) \quad (12.15)$$

so that the rate of change has the logistic's dependence on y modified by another second-degree equation in t . This is a difficult curve to work with, but is included here to show the range of possibilities generated through a variety of assumptions about the rate of change and all built around the deviation from the asymptote, $y - A$.

A popular curve for representing growth of individuals is named after Gompertz, whose interest was, however, in studying mortality curves for actuarial purposes. The equation is:

$$y = A \exp(-Ce^{-Bt}) \quad (12.16)$$

with derivative:

$$\frac{dy}{dt} = BC ye^{-Bt} \quad (12.17)$$

This is evidently a departure from the rates-of-change thus far considered. An inspection of data may be most convenient in terms of a relative rate of change.

$$\frac{dy}{ydt} = B e^{-Bt}$$

which might conveniently be plotted on "semi-log" paper (i.e., plot $\Delta y/y$ against t) where it should appear as a straight line. Referring back to equation (12.13) it appears that the relative rate of change of the logistic curve should provide a straight line in arithmetic coordinates:

$$\frac{dy}{ydt} = B - \frac{B}{A} y$$

so that the two curves (logistic and Gompertz) provide a rather distinct contrast.

Growth of individual fish has been represented by a curve developed by Von Bertalanffy, with the equation being:

$$y = A(1 + C e^{-Bt})^3 \quad (12.18)$$

This curve has the derivative:

$$\frac{dy}{dt} = 3B(A^{1/3} y^{2/3} - y) \quad (12.19)$$

which is not so readily compared with the other forms. However, the original rationale for the curve does give an interesting interpretation. Von Bertalanffy proposed that the rate of growth of a fish depends on the difference between anabolism and catabolism, with anabolism being proportional to surface area and catabolism to body weight. If surface area is taken as proportional to weight over length, an approximation then is weight to the $2/3$ power and we have:

$$\frac{dw}{dt} = k_1 w^{2/3} - k_2 w$$

where the k_i are constants, and we thus have the general form of equation (12.19). An interesting, and useful, sidelight is that the relationship can be approximated in terms of the length of fish, giving an equation equivalent to (12.10). An alternative way to write equation (12.18) is:

$$y = A[1 + e^{-B(t-t_0)}]^3$$

so that t_0 becomes a parameter replacing C . This can also be done for the other equations involving C as a multiplier of the exponential term. Since t_0 is a constant, one can write:

$$e^{-B(t - t_0)} = e^{Bt_0} e^{-Bt} = C e^{-Bt}$$

where $C = e^{Bt_0}$. The advantage of using t_0 is that it provides an explicit symbol of the fact that this constant lets one shift the curve along the time axis.

Another quite different growth curve is the Johnson-Schumacher equation, which has been used mostly for tree growth:

$$y = A \exp\left(-\frac{B}{t+c}\right) \quad (12.20)$$

The derivative is:

$$\frac{dy}{dt} = \frac{By}{(t+c)^2} \quad (12.21)$$

and this provides another variant on the relationship between rate of change, time, and current level.

12.4 Projection models

Many population studies must deal with the situation where appreciable numbers of individuals are removed from a population, often annually, but also on a less-regular basis. Dealing with such situations accurately requires estimates of *absolute* numbers in the population and of removals. The models used here also require that the removals take place in a relatively short time interval, to avoid the complications of appreciable numbers of deaths from natural causes during the removal period.

Two models may be considered:

$$\begin{array}{ll} \text{I} & N_t = N_{t-1}\lambda - K_t \\ \text{II} & N_t = (N_{t-1} - K_t)\lambda \end{array} \quad (12.22)$$

In essence, model I assumes that removals, K_t , take place just before the census at time t , while the second model assumes that removals take place just after the census at $t-1$. Annual censuses are assumed in both cases. If we let S_1 denote survival from $t-1$ to reproduction, and S_2 denote survival from reproduction, R , to removal, K_t , then Model I can be written as:

$$N_t = (N_{t-1}S_1)RS_2 - K_t$$

so that $\lambda = RS_1S_2$, including reproduction and survival through two periods of natural mortality. However, if there is an appreciable loss between removal and the second census, then another survival rate needs to be introduced, and a bias is introduced.

Hence if we have estimates of absolute population size, and known removals in a short time period, the two models offer a way to estimate λ in the presence of removals. A very convenient way to proceed is to use a ratio estimate. In Model I:

$$\hat{\lambda} = \frac{\Sigma(N_t + K_t)}{\Sigma N_{t-1}} \quad (12.23)$$

Where the summation is over successive observations. An alternative is to use a least-squares approach. A difficulty is that the estimates of population size are serially correlated, i.e., N_{t-1} becomes N_t in the next time period. Eberhardt (1987) examined this problem by testing various approaches on sets of population growth data that did not involve removals. With such data it is possible to estimate the rate of change by log-linear regression, as discussed in Section 12.1. The ratio and least-squares (log-linear regression) estimates gave consistent results, as shown in Fig.12.1.

With such a high correlation between the two methods, it would appear that the ratio method is likely to give useful results. A remaining problem, however, is one of obtaining useful variance estimates, due to the serial correlation issue. One way to approach the problem is to use jackknifing, in which a set of estimates is obtained by dropping each of the n items from which λ is estimated in turn, and forming n estimates of λ from the sets with one item deleted. A variance is then computed from the n estimates. A comparison (Fig. 12.2) between the jackknife variance estimates and that from the least-squares fit suggests that the jackknife method gives comparable estimates, but can't always be depended on.

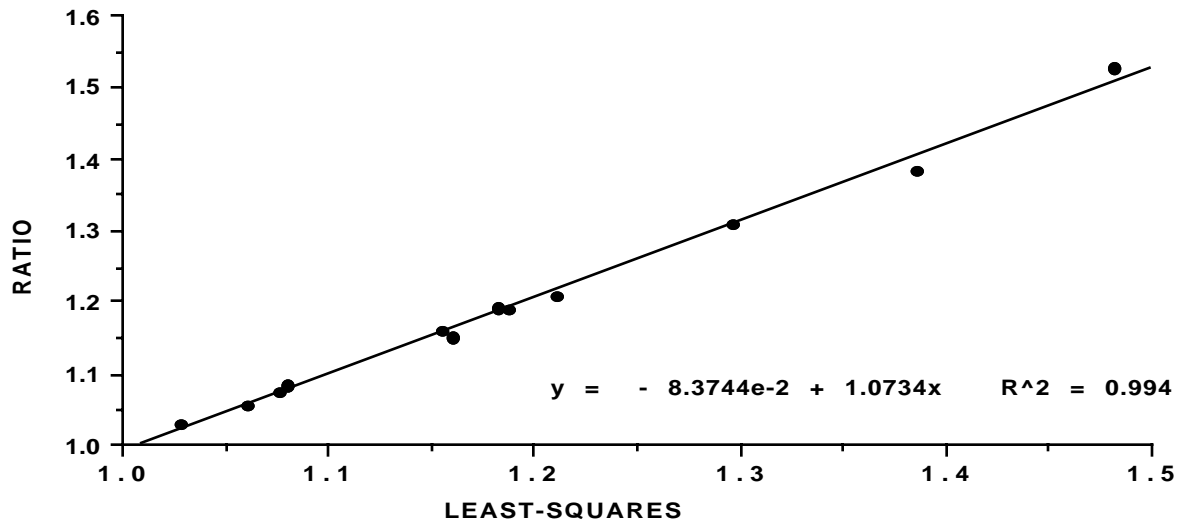


Fig. 12.1. Relationship between estimates of λ from the ratio method and from least-squares. Data from Eberhardt (1987:Table 2). 1:1 line shown.

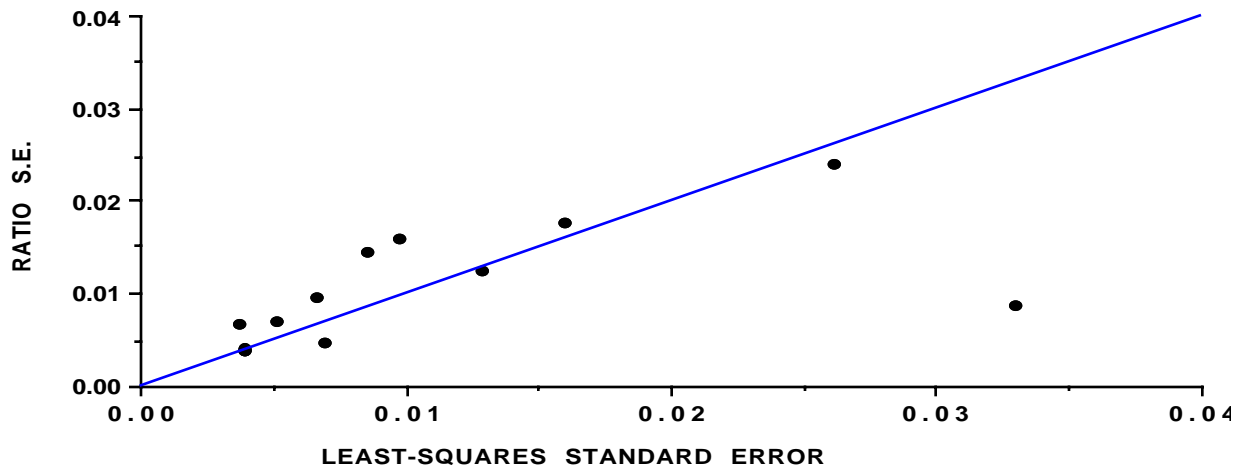


Fig. 12.2. Comparison of estimates of variance for λ obtained from jackknifing (Ratio S.E.) and estimates from a least-squares fit to the data. Data from Eberhardt (1987:Table 2). 1:1 line shown.

From the examples mentioned above, it appears that the projection models may be quite useful in various circumstances. In some instances, reproductive and survival data may also be available, so that an estimate of the

value of λ occurring without removals is also on hand. It will then be important to know whether an estimate of λ obtained from the removal data, as described above, is compatible with that obtained from the Lotka-Leslie approach.

12.5 Predator-prey models

Various simple models for predator-prey interactions have been discussed and explored mathematically for over 70 years. The initial models were two simple differential equations proposed by Lotka (1925) and Volterra (1931). Very little attention has been given to attempts to fit coefficients from actual field data, or to use such data to assess individual components of the models. Some prospects are explored in Section 12.6 by using data on wolves and their prey.

In practice, we usually need to deal with "birth-pulse" populations (Caughley 1977:6) where reproduction occurs in a relatively short period each year. The population then decreases until the next birth period, when it again gets a boost upwards. This sort of behavior may approximately be described by a "step-function", i.e., by a graph looking like a stairway, perhaps with steps of uneven size (cf. Fig. 11.1). One may thus use difference equations rather than differential equations, and the models used here are all computed as difference equations. Much of the recent literature is based on differential equations, which are not appropriate for birth-pulse populations because reproduction does not occur continuously throughout the year.

We first show the relationship of difference equations to differential equations, using the logistic equation (previously given as eq. (12.12) but shown here with the parameters familiar to ecologists):

$$\frac{dV}{dt} = rV[1 - \frac{V}{K}] \quad (12.24)$$

with K being the asymptotic value. Differential equations are often developed as a limiting expression, where some small increment of time approaches zero. For present purposes, we consider the increment as unity (one year, one day, etc.) and write:

$$\frac{dV}{dt} \approx V_t - V_{t-1} = rV_{t-1}[1 - \frac{V_{t-1}}{K}]$$

Rearranging gives a difference equation:

$$V_t = V_{t-1} + rV_{t-1}[1 - \frac{V_{t-1}}{K}] \quad (12.25)$$

Many of the differential equations of interest in ecology have no explicit solutions, but the logistic does:

$$V(t) = \frac{K}{1 + ce^{-rt}} \quad \text{where } c = \frac{K - x_0}{x_0} \quad (12.26)$$

with x_0 = initial value, here taken to be unity.

The logistic model for population growth assumes continuous growth, at an instantaneous rate, r . If we take $r = 0.8$ and $K = 30,000$, then we can plot eq.(12.26) for, say, 30 years. To approximate it with difference equation (12.25), we need to subdivide the year into increments. If we use 20 such increments, then $r_1 = \frac{r}{20} = \frac{0.8}{20} = 0.04$. Fig. 12.3 shows, the difference equation provides a reasonable approximation to the differential equation, with as few as 20 increments per unit of time.

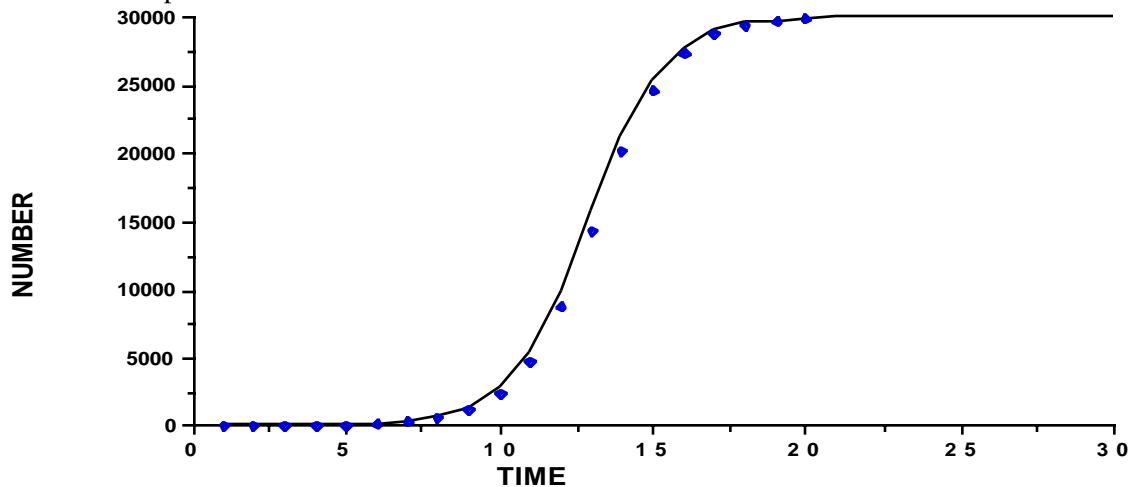


Fig. 12.3. Graph of a logistic equation (line) compared to values (points) from a difference equation version of the underlying differential equation.

Usually, we expect the behavior of the predator population to depend on the abundance of the prey, and it also may be subject to removals by man. The terms "prey" and "predator" often refer to animals, but the models can also serve to represent herbivores and vegetation. Consequently, we use the letters H for herbivores or predators, and V for vegetation or prey. The prey equation usually contains provision for self-limitation or a "density-dependence" term, often the logistic model given above, and then a term representing removals by the predators. This is termed the "functional response" and is denoted below as a generalized function, $F(H,V)$. The predator equation contains a term showing the way in which the predator supposedly responds to prey abundance, and this is termed the "numerical response" and denoted by $G(H,V)$. It is worthwhile to quote the original definition of these terms (Solomon 1949) inasmuch as some discussions in the literature appear to deviate appreciably from that definition. Solomon uses "natural enemy" to cover both predators and parasites:

"to be density-dependent, the enemy must respond to changes in numbers of the host The nature of this response is commonly twofold. First, there must be a functional response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host victims, or it will attack a fixed number more rapidly. A frequent, but not invariable result of this is an increase in the numbers of the enemy (a numerical influence) due to an increased rate of survival or of reproduction, or of both; this may or may not be sufficient to produce an increase in the proportion of enemies to the increasing hosts."

The two generalized equations are:

$$\frac{dV}{dt} = rV[1 - \frac{V}{K}] - HF(H, V) \quad (12.27)$$

$$\frac{dH}{dt} = HG(H, V) \quad (12.28)$$

Where $F(H, V)$ represents the “functional response” and $G(H, V)$ is the “numerical response”. In the early use of these equations, it was assumed that the functional response was proportional to the number of predators present, i.e., that $F(H, V) = \alpha V$ so that the equation becomes:

$$\frac{dV}{dt} = rV[1 - \frac{V}{K}] - \alpha VH \quad (12.29)$$

with the last term often interpreted as depending on an "encounter rate" and thus the product of the numbers of H and of V . The numerical response has been written as $G(H, V) = -d + \beta V$, and this can be interpreted as a constant mortality rate of predators (d) plus a reproductive rate depending on prey abundance (βV), with the equation then becoming:

$$\frac{dH}{dt} = (\beta V - d)H \quad (12.30)$$

There are a variety of other forms of functional and numerical responses, with a large literature dealing with theoretical interpretation of these terms. Various aspects of the theory appear in May (1981), and some of these are discussed in Section 12.7 below.

With this background, we can take a look at a system variously used to describe vegetation-herbivore interactions (Caughley 1976, 1977, Caughley and Lawton 1981), in which the herbivore has been described as an "ungulate" or as typifying "white-tailed deer colonizing a mosaic of grassland and forest" (Caughley and Lawton 1981). In the several examples, the relevant equations are given as differential equations, which are here translated to difference equations:

$$V_t = V_{t-1} + r_{m1} V_{t-1} (1 - \frac{V_{t-1}}{K}) - c_1 H_{t-1} (1 - e^{-d_1 V_{t-1}}) \quad (12.31)$$

$$H_t = H_{t-1} [1 - a_2 + c_2 (1 - e^{-d_2 V_{t-1}})] \quad (12.32)$$

The exponential terms, $(1 - e^{-d_1 V_{t-1}})$, are supposed to adjust the herbivore's intake of vegetation and population growth rate according to density of vegetation.

Plots of vegetation and herbivore density show rather dramatic changes in the first 20 years, and come nearly to equilibrium in 50 years (Caughley 1977:Fig. 9.6, Caughley and Lawton 1981:Fig. 7.3). If we plot the difference equations (12.31) and (12.32) using the constants given by Caughley (1977:129), we get very pronounced and continuing oscillations (Fig. 12.4).

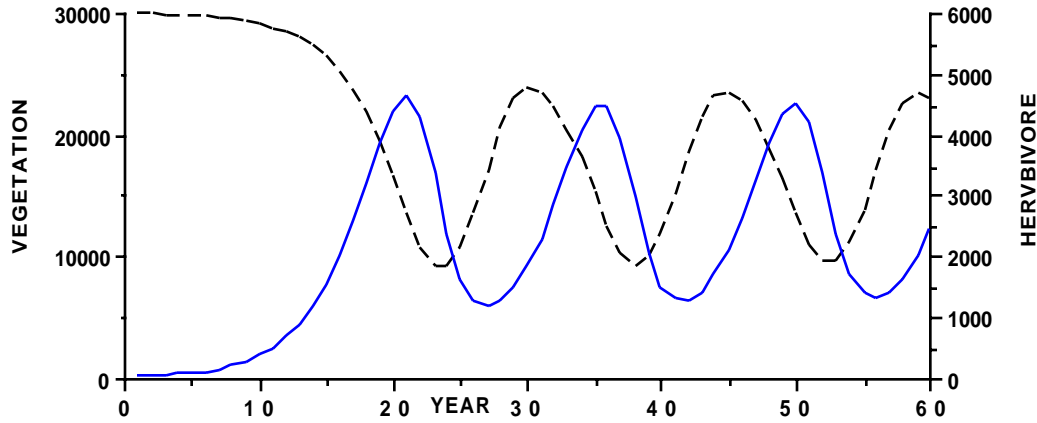


Fig. 12.4. Caughley's (1977) vegetation-herbivore system computed as a difference equation in which reproduction occurs annually.

Why the difference? The answer lies in the way in which the equations interpret reality. The difference equations assume reproduction occurs just once a year for the herbivore and for vegetation. The differential equations assume reproduction goes on throughout the year. Caughley (1977:130) remarked that "the population has been grown in a programmable desk calculator by estimating growth curves twenty times per year and adding on the appropriate increment each time". However, ungulates don't reproduce 20 times a year, behaving instead like the difference equations, producing young once a year. Since vegetation does grow continuously over part of the year, a somewhat different model presumably could be used for vegetation. If we follow Caughley's prescription cited above, using difference equations and rates divided by 20, then the difference equation model reflects his Fig. 9.6 reasonably well, but the time scale is now multiplied by 20. In effect, if reproduction occurs only once a year, then the curve shown by Caughley takes something like 500 years, not 50 years.

The main point to be made here is that one needs to be sure that the equations used do reflect the biology of the situation at hand. Some other problems with the system discussed above are described by Eberhardt (1988). Another example concerns an effort to consider the role of interactions between species in the management of multispecies fisheries. May et al. (1979) used differential equation models to illustrate the possible impacts of commercial harvesting of the main food supply (krill) of baleen whales in Antarctic waters. They stated that "A crude Lotka-Volterra form of predation is assumed, with prey being consumed at a rate proportional to their density, aN_1 , per predator". Written as a difference equation, this gives:

$$V_t = V_{t-1} + r_1 V_{t-1} \left(1 - \frac{V_{t-1}}{K}\right) - c_1 H_{t-1} V_{t-1} \quad (12.33)$$

while their predator equation is:

$$H_t = H_{t-1} + r_2 H_{t-1} \left[1 - \frac{H_{t-1}}{a V_{t-1}}\right] \quad (12.34)$$

The problem is that baleen whales are very unlikely to have evolved to each take a proportional share of the available prey. Instead they quite clearly take as much prey as needed to supply the individual whale, so that the last term in eq. (12.33) becomes $c_1 H_{t-1}$. Such a change makes an appreciable difference in trend of the predator and prey curves, and conclusions about equilibrium points, relative yields, and the like, as indicated in Eberhardt (1988).

12.6 A wolf-ungulate model

As noted above in connection with eq. (12.33), it is unlikely that an effective large predator will take a proportional share of the available prey. A further modification of eq.(12.33) is available in the form of the generalized logistic in which the growth rate may not begin to decline appreciably until the population approaches its asymptotic value (K). With these modifications, eq. (12.33) becomes:

$$V_t = V_{t-1} + r_1 V_{t-1} [1 - (\frac{V_{t-1}}{K})^z] - c H_{t-1} \quad (12.35)$$

The general form of eq.(12.34) has been recently popular under the label of "ratio dependence" (Matson and Berryman 1992). Eberhardt (1997) used data on moose and caribou from the literature to show that the functional relationship very likely can be reduced to the constant, c , of eq.(12.35). It is worth noting here that the equilibrium values (obtained by setting $H_t = H_{t-1}$ and $V_t = V_{t-1}$ are:

$$V = K[1 - \frac{ca}{r_1}]^{1/z} \quad \text{and} \quad H = aV \quad (12.36)$$

The best available data are those for moose. Eberhardt (1997,2000) used data from the literature to estimate c in eq. (12.35) as 2 moose killed per wolf per 100 days in winter, with an annual rate of a little less than 7 moose per wolf. Eberhardt (1998) calculated a maximum rate of increase for moose as $\lambda = 1.38$. The parameter z is not well established, but was used as $z = 5$. Carrying capacity (K) depends on the specific population considered and thus may be selected arbitrarily here. For eq. (12.34) the maximum rate of increase for wolves was estimated as $\lambda = 1.48$ (Eberhardt 1998) and the ratio-dependence constant as $a = 1/20$ wolves/moose (Eberhardt and Peterson 1999). Using these constants, and starting with a moose population of 30,000 (at carrying capacity, K) and a small initial wolf population (20) gives the results of Fig. 12.5, which can be compared to Fig. 12.4. A small initial fluctuation soon disappears and both moose and wolves settle down to steady-state numbers at the assumed ratio of 20 moose per wolf.

An obvious feature of Fig. 12.5 is the absence of the oscillations that were induced in the model of Fig. 12.4 by the choice of mathematical forms for the functional and numerical responses. There is a good deal of evidence that such oscillations do in fact occur in insect populations with their generally high rates of increase, but wolves and their prey have much lower rates of increase so that the models derived for insects and other species with high rates of increase ought not to be arbitrarily assumed to be appropriate as seems to have been done in the literature.

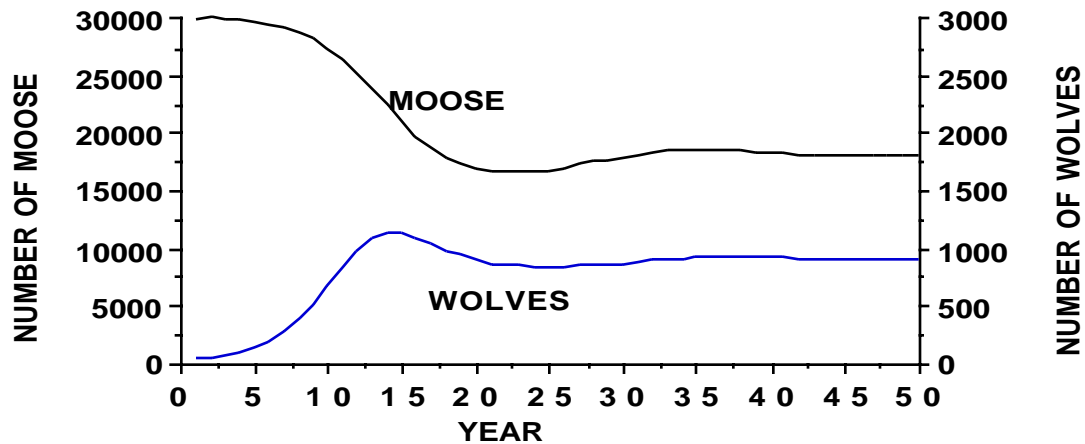


Fig. 12.5 Trend of moose and wolf populations using Eq. (12.34) and (12.35) with the parameters given above.

Another carryover from entomological studies is the notion of a “total response” model in which the predator population is assumed to respond instantaneously to changes in prey abundance. Using such a model one can conveniently depict predator abundance as a function of prey abundance and produce a variety of models along the lines of Messier (1994). However, wolves do not respond instantaneously to fluctuations in prey numbers, and hunting, trapping, and “control” actions have resulted in non-equilibrium numbers of predator and prey in most real-world situations. A realistic approach thus needs to depend on equations like (12.34) and (12.35) that show non-equilibrium conditions. The “total response” model traces back to Holling (1959) who warned about the consequences of assuming that model as follows: “The method is an over-simplification, since predator density is portrayed as being directly related to prey density. Animal populations, however, cannot respond *immediately* to changes in prey density, so that there must be a delay of the numerical response” and “the total response obtained when prey or hosts are steadily increasing will be different than when they are steadily decreasing. The amount of difference will depend on the magnitude and amount of delay of the numerical response, for the functional response has no element of delay”.

An interesting aspect of the model of eq. (12.34) and eq. (12.35) is that it can be fit directly to actual data, using multiple regression. An attempt to do so for data on Isle Royale moose and wolves appears in Eberhardt (1998:Fig. 2). Unfortunately, there are few data with enough years of observations on both prey and predators to make such an approach widely applicable and both moose and wolves on Isle Royale appear to have been subjected to influences not considered in the simple model. This illustrates the major dilemma in model-building in ecological studies. Usually only a few parameters can be unambiguously estimated from actual data, forcing the use of simple models that cannot accommodate unexpected changes due to environmental or other factors. A further possible difficulty with the simple model of eq. (12.34) is the assumption that wolf abundance is limited solely by moose abundance through the ratio-dependence parameter (a). In reality, wolf packs defend more or less

exclusive territories, a factor that may limit their abundance in the presence of high prey densities.

12.7 Assessing differential equation models

This Section is provided to supply an indication of how differential equation models for predator-prey studies can be evaluated. The basic problem is that most such equations cannot be “solved”, i.e., integrated. Section 12.5 used the logistic equation as an example of a differential equation that can be solved directly and showed that the difference equation analog can be used to provide a good approximation to the behavior of the differential equation. This is the simplest approach for studying differential equations when direct solutions are not possible. Quite a bit can be learned about the equations by plotting trend of the populations on a diagram showing the “isoclines”. We can illustrate the basics by considering a modification of the original predator-prey equations due to Lotka (1925) and Volterra (1931). The original equations are:

$$\begin{aligned}\frac{dV}{dt} &= r_1 V - bVH \\ \frac{dH}{dt} &= cVH - dH\end{aligned}$$

where V denotes prey and H denotes predator as before. According to May (1981) “This system has pathological dynamical properties...”, and we will not consider the equations in the above form further here. A major problem from the biologist’s point of view is that, when no predators are present ($H = 0$), the prey population will grow continuously, without limit. Hence early workers made the modification given by eq. (12.29) which introduces the logistic equation as a control on the prey rate of increase if no herbivores are present, i.e.,

$$\frac{dV}{dt} = r_1 V \left[1 - \frac{V}{K}\right] - bVH$$

One approach to studying differential equations of this type is to plot the trend of equilibrium solutions, i.e., let $dV/dt=0$, and thus:

$$H = \frac{r_1}{b} \left[1 - \frac{V}{K}\right]$$

so that, given values of the constants, one can plot H against V as a straight line. The solution of the predator equation is just $V = d/c$, a constant, and thus a vertical line on the plot of H against V . The intersection of the two lines (known as isoclines) provides an “equilibrium point” or the joint solution of the two equations. This is the point at which the predator and prey populations settle down to constant values (equations are known that cycle endlessly, and one example will be given later in this Section).

To go further, we need to convert the differential equations to difference equations. This is done by replacing dV/dt by $\Delta V/\Delta t$ where Δ

represents a small increment. In the case of approximating the logistic equation in Section 12.5, we could make this increment as small as we like, but the predators and prey mainly considered here reproduce only once a year, so the time increment needs to be one year, i.e., $\Delta t=1$ and $\Delta V = V_t - V_{t-1}$, or the size of the prey population at time t minus its size at time $t-1$. The difference equation for the prey population then becomes that of eq. (12.33) and the predator equation is:

$$H_t = H_{t-1}[1 - d + c_2 V_{t-1}] \quad (12.37)$$

This is the same as equation (12.30) but now is written as a difference equation. These equations are readily plotted in EXCEL, using values supplied here. For convenience in making comparisons and for discussion purposes, parameters used in the following examples are standardized so as to give roughly equivalent equilibrium values and to approximate values for moose and wolves used by Eberhardt (1997, 1998) and Eberhardt and Peterson (1999). The equilibrium values are approximately 4000 moose and 200 wolves, while initial values are 8000 moose and 50 wolves. Where an asymptotic prey value is needed, it is set at $K = 10,000$. Maximum rate of increase for prey is $r_1 = 0.38$ and $r_2 = 0.48$ for predators. For eq.(12.33) the take by wolves is assumed proportional to number of prey present. This is not a very realistic assumption as wolves generally are likely to be capable of taking what they need as suggested in Section 12.6, in connection with eq. (12.35). In that equation, a constant rate is assumed and is set at $c = 5$ below. For comparability we thus assume that $c_1 V = 5$ in eq. (12.33) where V is the equilibrium moose population, so that $c_1 = 5/4000 = 0.00125$. In the prey equation [eq. (12.37)] d is regarded as an annual wolf mortality rate and set at $d = 0.40$, while c_2 denotes a kind of reproductive rate, being the gain realized from consuming moose. At equilibrium we have $c_2 V = d$, i.e., the gain to the wolf population just offsets loss (d), so we set $c_2 = 0.40/4000 = 0.0001$.

The various equations are readily computed and plotted in EXCEL, using the values supplied here. One starts out with initial conditions for predator and prey, $V_0 = 8000$ and $H_0 = 50$, and uses the parameters given above. Thus in eq.(12.33) the observation for prey at time 1 is:

$$V_1 = V_0 + r_1 V_0 \left[1 - \frac{V_0}{K}\right] - c_1 V_0 H_0 = 8000 + 0.38(8000)\left(1 - \frac{8000}{10000}\right) - 0.00125(8000)50 = 8108$$

while the predator number [eq.(12.37)] is;

$$H_1 = 50[1 - 0.4 + 0.0001(8000)] = 70$$

and at time 2 the prey number is:

$$V_2 = V_1 + r_1 V_1 \left[1 - \frac{V_1}{K}\right] - c_1 V_1 H_1 = 8108 + 0.38\left[1 - \frac{8108}{10000}\right] - 0.00125(8108)70 = 7981.5$$

Subsequent terms are computed in the same manner, and a plot of predator and prey can be obtained as in Fig. 12.6, which shows the course of the populations over time. We can also plot predator numbers against prey numbers along with the isoclines $H = 304[1 - 304V/10000]$ and $V = 0.4/0.0001 = 4000$ getting Fig. 12.7. In this example, the two populations oscillate over more

than 100 years and ultimately settle down at the intersection of the isoclines, i.e., 4000 prey and about 180 predators.

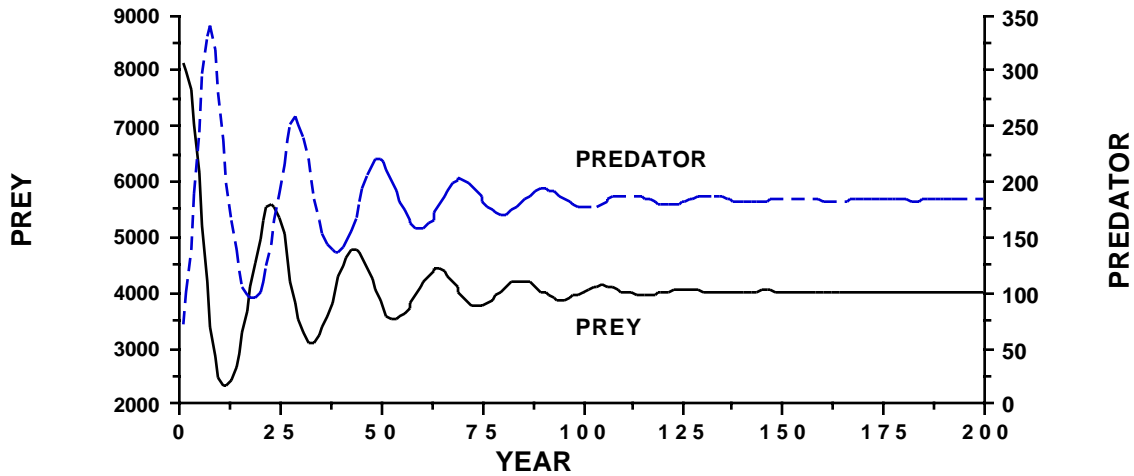


Fig. 12.6 Course of predator and prey populations calculated from equations (12.33) and (12.37).

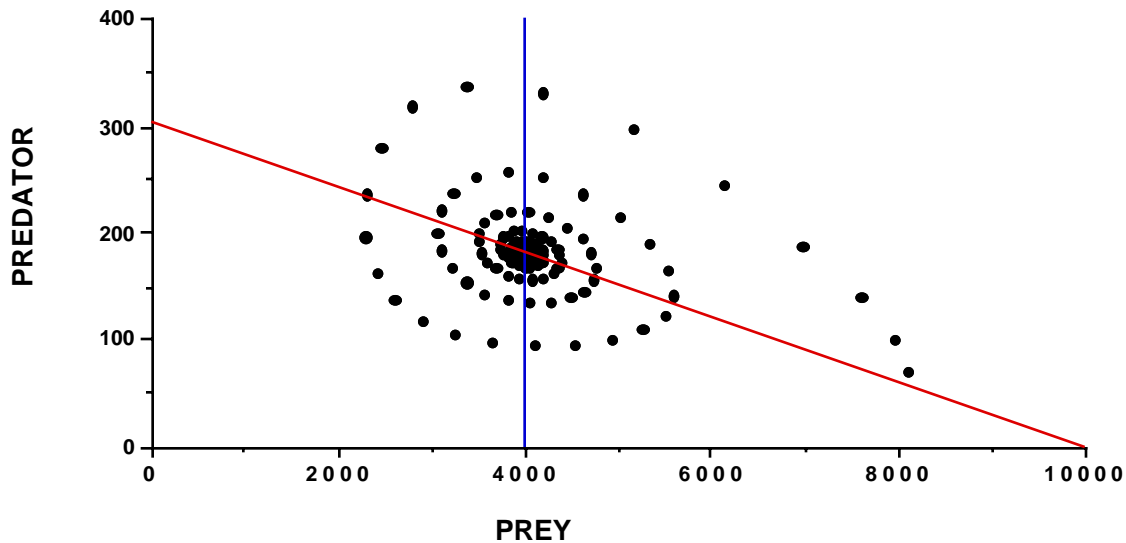


Fig. 12.7 Diagram showing isoclines (lines). Course of populations is shown by the spiral of points starting near initial values (50 predators, 8000 prey) and ending near junction of isocline lines (equilibrium values).

The dramatic fluctuations generated by the above equations have been observed for insect populations, and might well be invoked for some vertebrate populations that show cycles of varying lengths, but it is not established as yet that such observed cycles are necessarily due to predator-prey interactions. It is thus useful to look at a few equations that do not vary so dramatically. One set is that given by eqs.(12.33) and (12.34) and used by May et al. (1979) to model Antarctic food chains. A diagram (Fig. 12.8) showing isoclines for these equations shows only one simple curve to the equilibrium

point from the initial numbers (8000 prey and 50 predators), and the population plots (Fig. 12.9) show essentially one cycle before settling down.

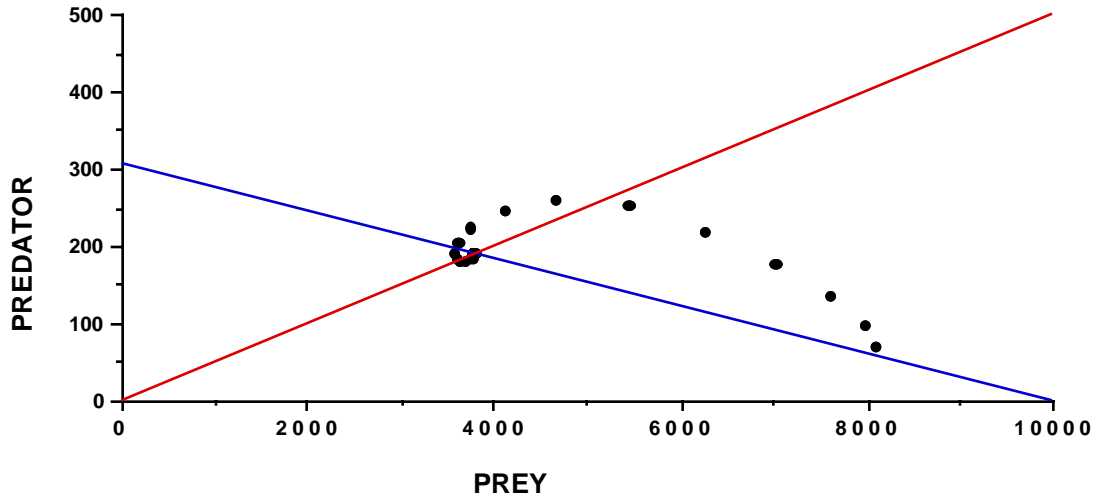


Fig. 12.8 Isoclines and trace of points for equations (12.33) and (12.34).

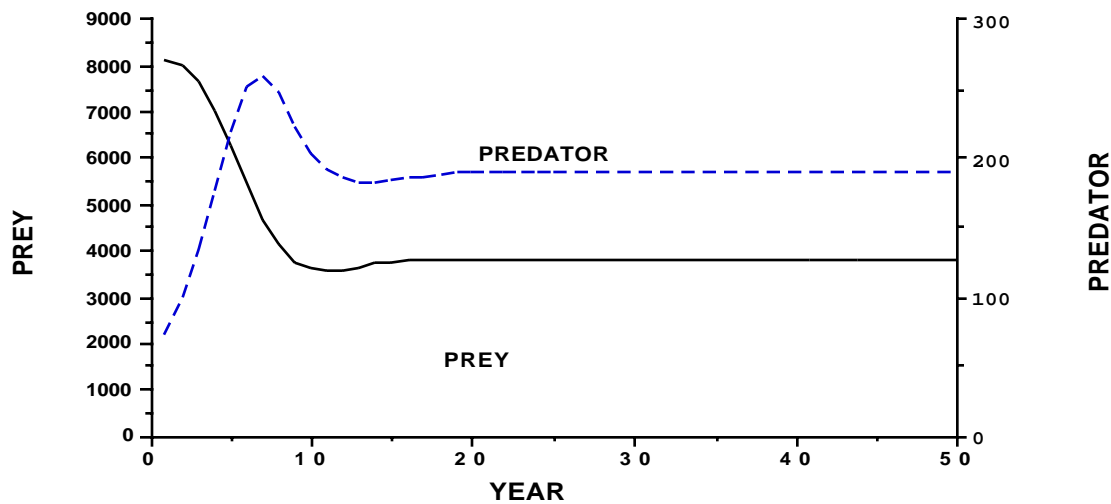


Fig. 12.9 Population trace for equations (12.33) and (12.34).

In connection with equations (12.33) and (12.34) it was remarked (Section 12.5) that the last term in eq.(12.33) very likely should not include the prey, i.e., that large predators like baleen whales and wolves most likely take what prey they need rather than taking prey in proportion to its abundance. Thus the modified equation was used as eq. (12.35) in the wolf-ungulate model of Section 12.6, with one further modification, which was to change the logistic term in the prey equations above to a “generalized logistic”:

$$\left[1 - \left(\frac{V_{t-1}}{K}\right)^z\right]$$

where the exponent, z , is equal to or greater than unity (set at unity it gives the usual logistic term). This modification is essential in that it gives prey

populations a much more nearly constant rate of increase until they approach the asymptote. If the rate of increase is permitted to decrease linearly as in the usual logistic model, then prey populations cannot stand much in the way of predation. The population course for this set of equations [(12.34) and (12.35)] is very much the same as in Fig. 12.9, but the isocline lines now differ (Fig. 12.10), in that the equilibrium solution for the prey equation produces a curve which is a second degree polynomial for $z=2$, but would be a third degree polynomial if $z=3$, and so on. Note that using $z=2$ has increased the equilibrium values substantially, due to use of the generalized logistic rather than the ordinary logistic which was used in producing Fig. 12.8

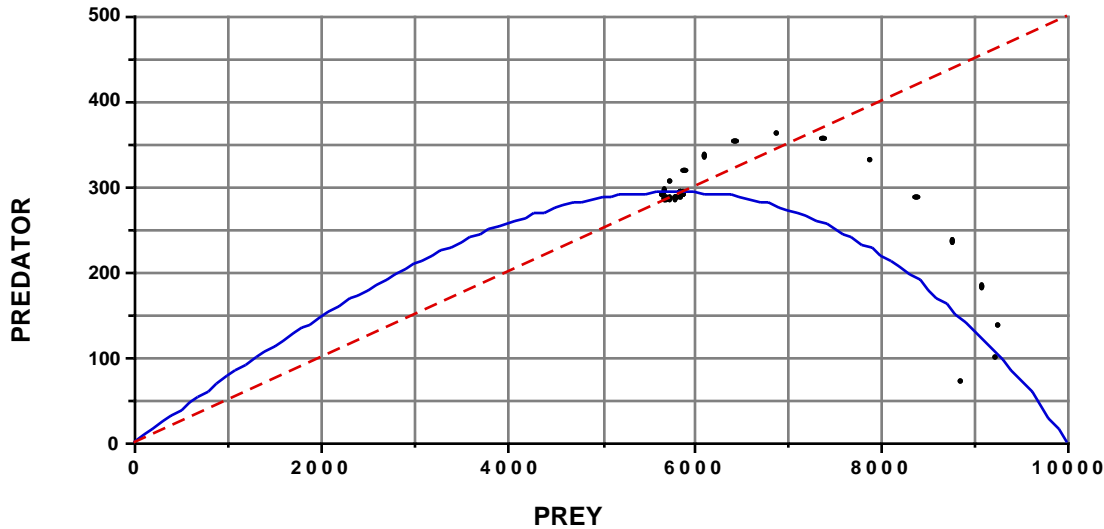


Fig. 12.10 Isocline lines and population plot for equations (12.34) and (12.35).

Another version of the prey equation may be considered at this point. This incorporates the widely-used functional relationship originated by Holling (1959), and usually described as his Type II curve. This gives rise to the following prey equation:

$$V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \frac{V_{t-1}}{K} \right] - \left[\frac{m V_{t-1}}{w + V_{t-1}} \right] H_{t-1} \quad (12.38)$$

The functional relationship contains two parameters, m and w , and gives rise to a curvilinear relationship replacing the very simple constant, c , of eq. (12.35). The parameter m was set at 5 and $w = 1000$. The population trend is again a simple curve (Fig. 12.11) and the isoclines are much like those of Fig. 12.10. The Type II curve is not very much different from an exponential curve, as can be shown by series expansions:

$$\frac{mV}{w+V} = m \left(1 + \frac{w}{V} \right)^{-1} = m \left[1 - \frac{w}{V} + \left(\frac{w}{V} \right)^2 - \left(\frac{w}{V} \right)^3 + \dots \right]$$

$$me^{-\frac{w}{V}} = m \left[1 - \frac{w}{V} + \frac{\left(\frac{w}{V} \right)^2}{2!} - \frac{\left(\frac{w}{V} \right)^3}{3!} + \dots \right]$$

When V is large, as it is for the most part here, these two expressions give very similar curves. Using $m=5$ and $w=1000$ as used here, the Type II curve is much the same as an exponential with the same parameters (Fig. 12.12). The agreement is worth noting mostly by way of suggesting that one not place too much faith in the derivations of the Type II curve found in the literature.

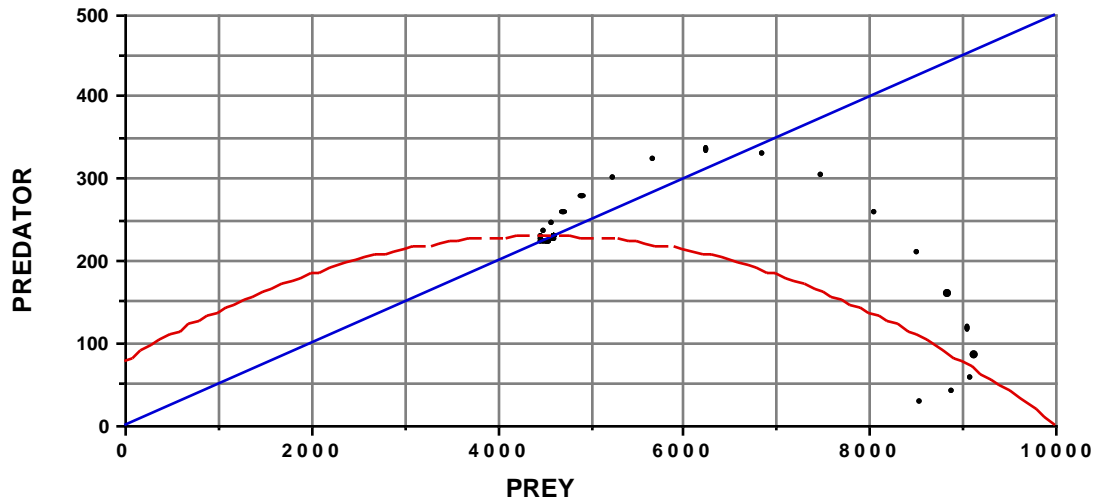


Fig. 12.11 Isoclines and population trend for equations (12.38) and (12.34).

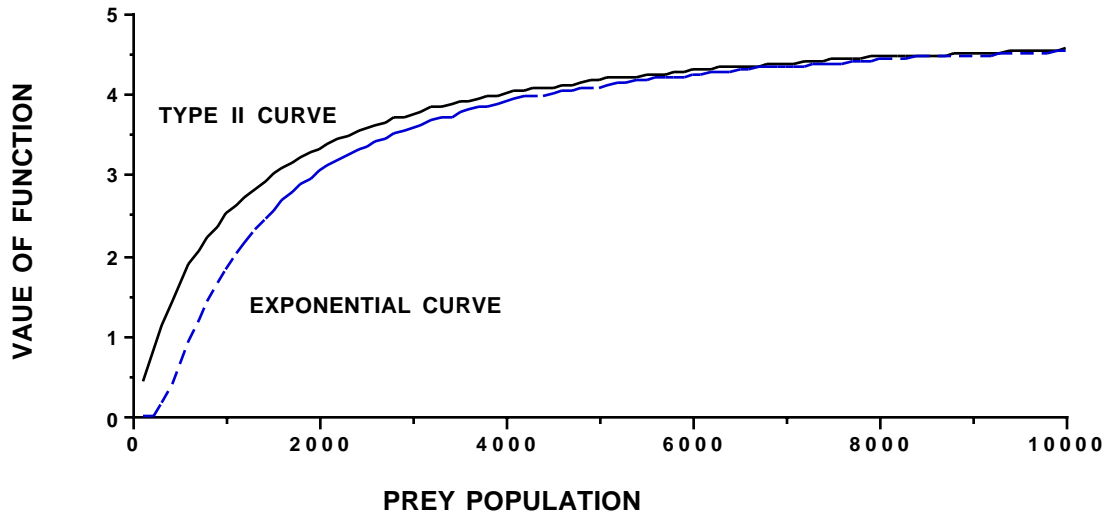


Fig. 12.12 Comparison of Hollings Type II curve and an exponential function with the same parameters.

Thus, although we have used a different model for prey, the general results are much the same as for 3 earlier cases. However, if we follow what seems to be the current trend in the literature and use the same curve for functional and numerical response, then a very different result is obtained, i.e., sustained oscillations of the form exhibited in Fig. 12.4. The prey equation now is:

$$H_t = H_{t-1} \left[1 + \frac{c_3 m V_{t-1}}{w + V_{t-1}} - d \right] \quad (12.39)$$

The combination of eqs.(12.38) and (12.39) yields dramatic and continuing oscillations and does not appear to converge on equilibrium values (Fig. 12.13). Also, different starting values of predator and prey give different results. Hence these curves are not considered further here. Readers interested in the theoretical basis for such curves should consult May (1981) and the current literature on predator-prey models. Their practical utility remains to be demonstrated.

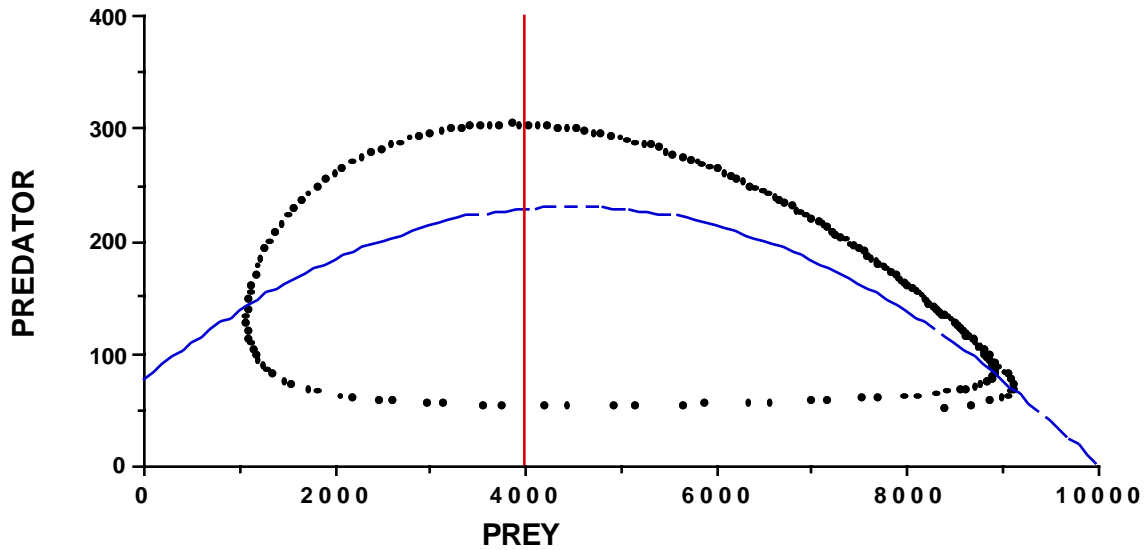


Fig. 12.13. Trace of points generated by eqs. (12.38) and (12.39).

From the results considered thus far, it appears that the ratio dependence model for predators [eq.(12.34)] yields rather stable results when combined with various models for prey abundance, and that the prey equation used for moose and wolves [eq.(12.35)] may be presently most useful for actual data on large vertebrate predator-prey studies. However, most ungulate populations are preyed on by hunters, as well as by wolves. Consequently, it is worthwhile to consider a modification of eq.(12.35) that brings in removals by hunters:

$$V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - c H_{t-1} - R \quad (12.40)$$

Here, we assume a constant annual harvest of, say, moose by hunting, set for convenience at 290 individuals per year. Utilizing eq.(12.34) for predators, population trends are qualitatively much the same as before with the populations approaching equilibrium in about 20 years. The isocline diagram (Fig. 12.14) differs, however, in several respects from Fig. 12.10, which represents the situation without hunting removals. The equilibrium values are substantially lower with both prey and predator numbers reduced, and the isocline lines just intersecting rather than crossing. Perhaps the most interesting and instructive result comes if we increase the hunter harvest just

slightly—from 290 per year to 294 per year. This results in a crash of both populations (Fig. 12.15), after a long, rather slow decline. Of course, if the harvest is set a little larger, the crash occurs sooner. These equations should not be taken as useful direct models of actual populations, inasmuch as they are very sensitive to small changes in parameters. In reality, wolves will most likely “switch” to alternate prey if possible or leave the area entirely. The general picture is well-illustrated by the fate of the Nelchina caribou herd in Alaska, which became very large during wolf control, but ultimately crashed when wolves regained high numbers and a largely fixed hunting harvest was maintained. Some details of this event were reported by Eberhardt and Pitcher (1992). A very considerable controversy about likely causes is discussed in references cited in that paper.

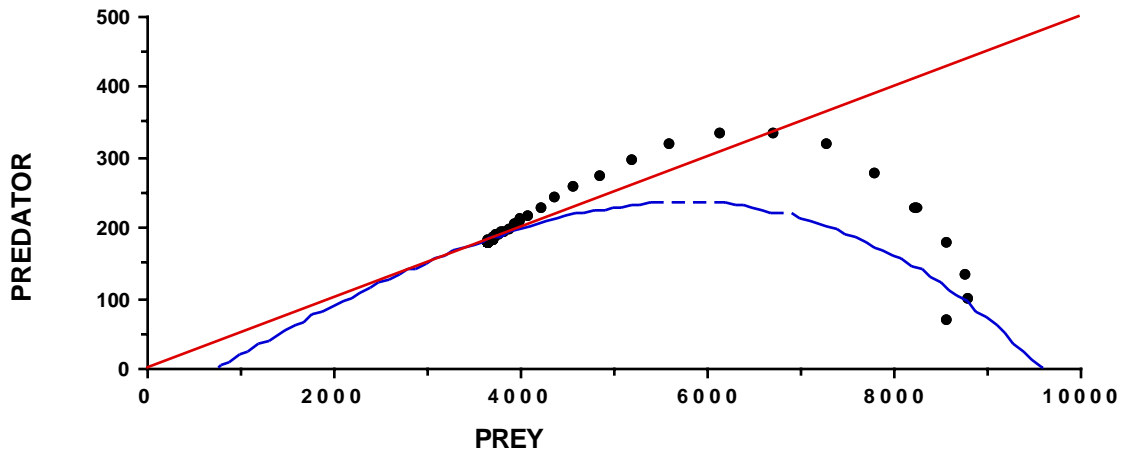


Fig. 12.14. Isocline lines and population plot for equations (12.34) and (12.40).

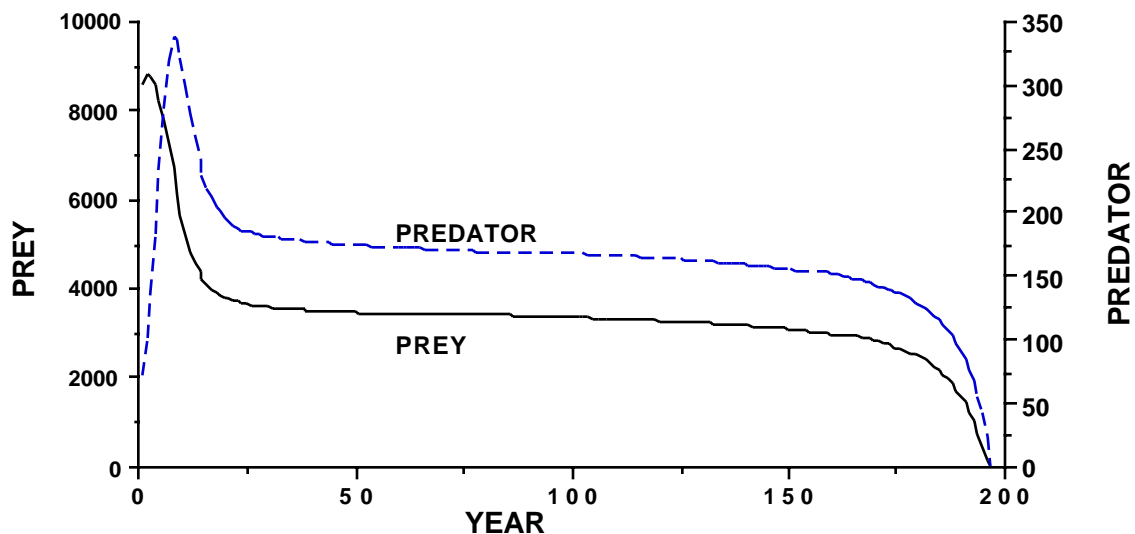


Fig. 12.15 Trend of predator and prey populations when hunter harvest is high enough to ultimately result in a crash of both populations.

Up to this point, we have considered some problems in predator-prey models (Section 12.5), looked briefly at a wolf-ungulate model (Section 12.6),

and then delved deeper into the various differential equation models in the present Section. A tentative conclusion from the review here is that the equations of Section 12.6 seem to “behave” reasonably well in comparison with some popular versions. It may thus be desirable to provide more detail on the evidence supporting that model. For convenience the underlying difference equations are repeated here.

The prey equation is:

$$V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - c H_{t-1} \quad (12.35)$$

and the predator model is:

$$H_t = H_{t-1} + r_2 H_{t-1} \left[1 - \frac{H_{t-1}}{a V_{t-1}} \right] \quad (12.34)$$

while the equilibrium conditions are:

$$V = K \left[1 - \frac{ca}{r_1} \right]^{1/z} \quad \text{and} \quad H = aV \quad (12.36)$$

Definitions and some likely parameter values were given in Section 12.6. Here we look briefly at the data supporting these models and the parameters.

Evidence for the constant, c , in eq.(12.35) has been collected from a number of sources (Fig. 12.16) that suggest the moose kill/wolf/100 days to be nearly constant over a wide range of moose densities.

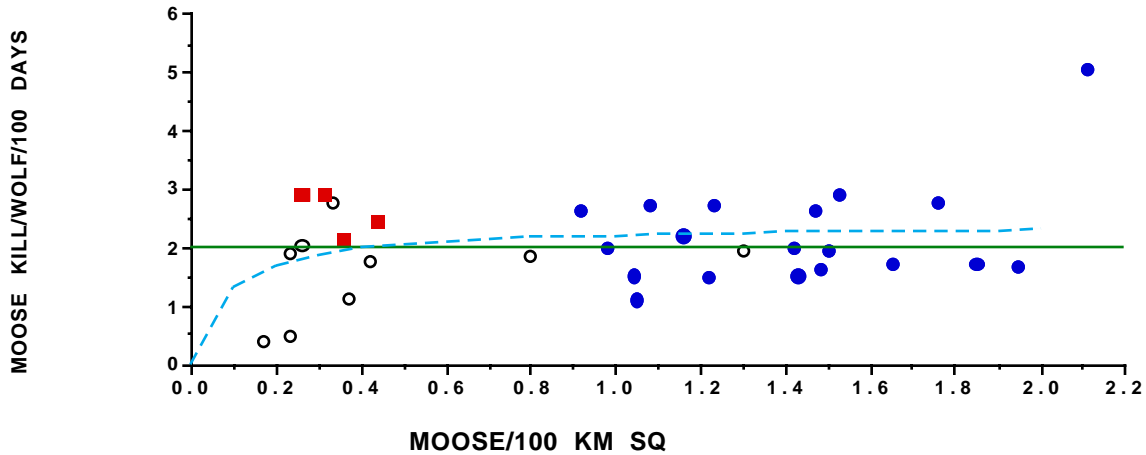


Fig. 12.16. Data on moose kill per wolf per 100 days in winter from Eberhardt (2000) with data (solid square symbols) from Hayes and Harestad (2000) added. Solid circles represent individual year data from Isle Royale and open circles show data of Messier (1994: Table 2). Solid line shows constant rate assumed here, from an average that does not include two very low and one very high point. Broken line shows fit of Type II curve.

Some lower kill rates at low moose densities might be taken as evidence for the Type II model used in eq. (12.38). That model has been fitted to the data with non-linear least-squares as shown in Fig. 12.16. As was noted in connection

with Fig. 12.11, introducing the Type II curve does not appear to change behavior of the equations significantly. Arbitrary values of the parameters m and w were used in eq. (12.38) to give results compatible with most of the other equations. Using actual data now gives quite different values, namely $m = 2.38$ and $w = 0.082$.

The other important evidence for the model suggested here has to do with the ratio dependence constant, a , in eq. (12.34). The arguments for this model were described in more detail by Eberhardt and Peterson (1999). A possible improvement offered here is that the underlying relationship between rate of increase for wolves (λ) and the wolf/moose ratio may be curvilinear, with an intercept at a somewhat lower wolf/moose ratio, changing the equilibrium value from about 20 moose/wolf to 24 moose/wolf (Fig. 12.17).

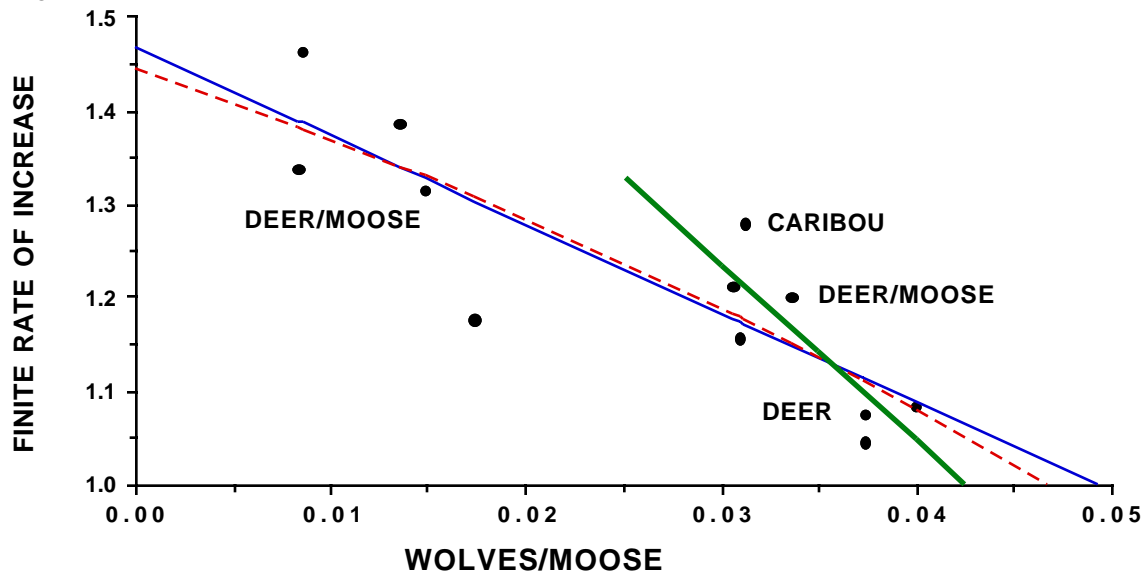


Fig. 12.17. Finite rate of increase (λ) of wolf populations vs. observed wolf-moose ratios. The broken line depicts a second degree polynomial fitted to the data, and the short regression line has been fitted to the data from the 7 highest moose-wolf ratios to approximate what may be an underlying strongly curved relationship. Sources of the data appear in Eberhardt (1998) and Eberhardt and Peterson (1999).

The best support for eq. (12.35) comes from the trend of the moose population on Isle Royale, Michigan (Fig. 12.18). In the early stages of the study it appeared that the wolf population was controlling moose abundance, with the two populations approaching equilibrium by about 1979 (Eberhardt and Peterson 1999). However, the wolf population “crashed” in 1980, very likely in consequence of the arrival of a virus (parvovirus) in the population. Moose numbers then increased steadily and the moose population ultimately also crashed in a severe winter. An epizootic of winter ticks (Delgiudice et al. 1997) interrupted the steady growth of the moose population in 1988, so eq.(12.35) has only been fitted up to that point.

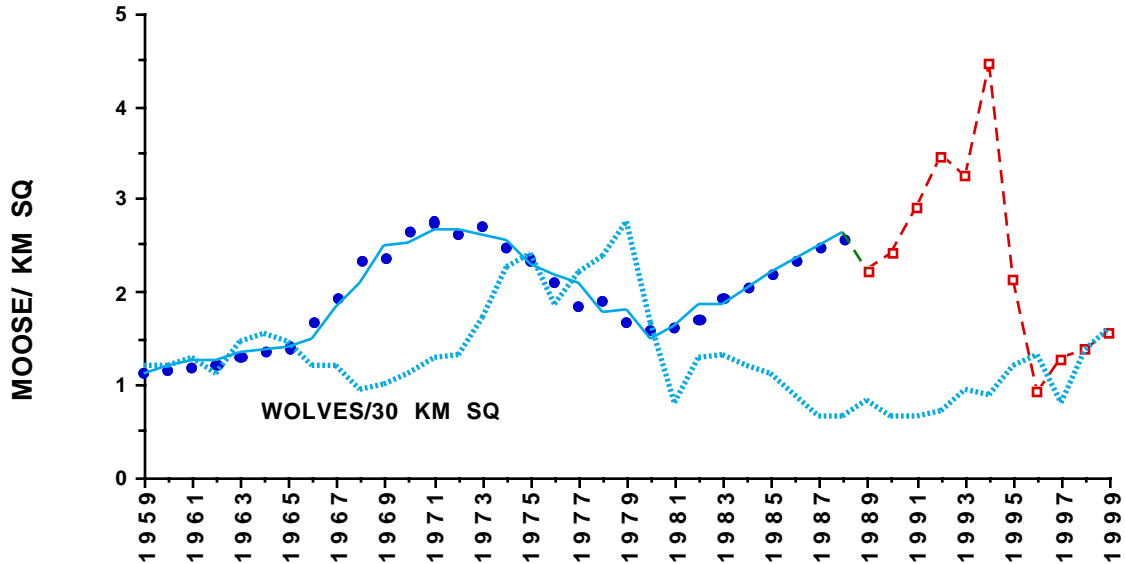


Fig. 12.18. Trend of the Isle Royale moose population. Solid points and a solid line show moose abundance through 1988 and the fit of eq.(12.35) to the data. Open symbols show estimated moose numbers from 1989 onwards and the estimates are connected by a dashed line to show the recent trend. Wolf density is shown by a broken line.

12.8 EXERCISES

12.8.1 Non-linear least-squares. The following are the data from Fig. 9.3 (muskox population growth curve). Fit the loglinear regression model of eq. (12.5) using the analysis toolpak of EXCEL. Then explore non-linear least-squares fitting of the same data by making a table bordered by values of the two parameters and calculating the sums of squares for trial values of the parameters. Calculate the sums of squares from:

$$S = \sum [y_i - (a \exp(bx_i))]^2$$

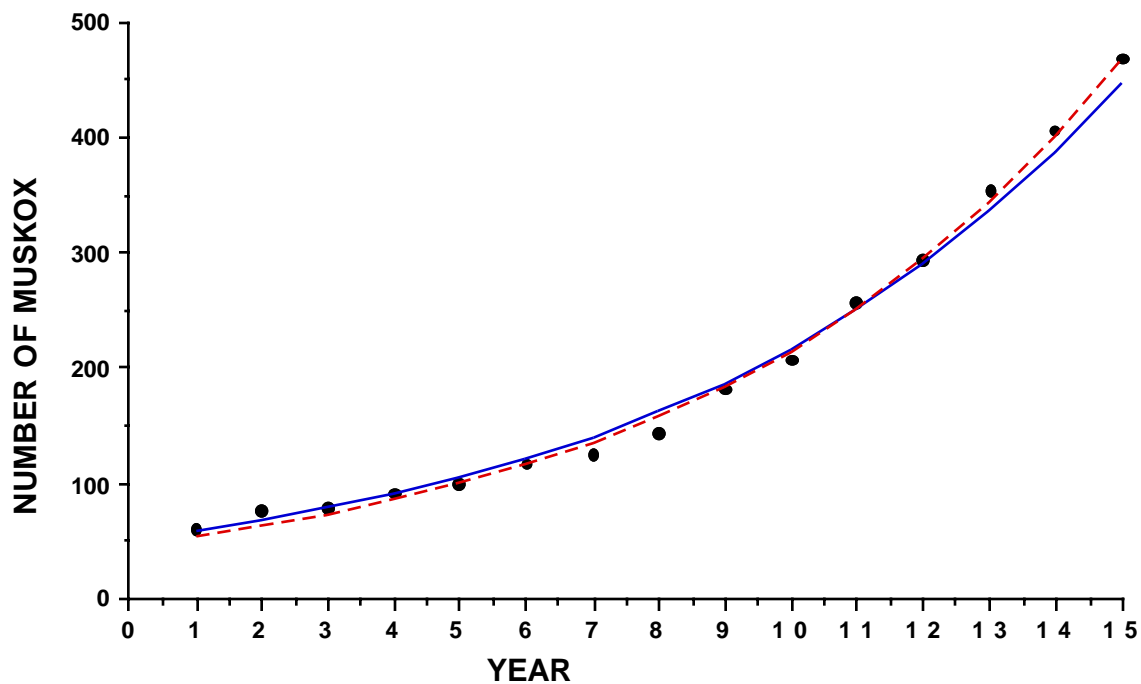
You will need trial values of a and b , and these can be taken from the loglinear fit. It can be a tedious undertaking unless you start out with trial values, put the sum of squares in a table and border these with sums of squares from the adjacent values of a and b . Use 3 decimal places for b and 2 digits for a (don't forget that the loglinear fit gives $\log a$ as the intercept, so you have to transform back). You can map the sums of squares and trace the minimal sums of squares until you find one that is the lowest in its region. Sometimes this "brute force" approach is useful if you don't have ready access to a computer program that provides nonlinear least-squares estimates. If you do have access to such a program, use it to check your results.

The data are:

YR	NUMBER
1	61
2	76
3	77
4	90

5	100
6	116
7	126
8	143
9	181
10	206
11	256
12	293
13	353
14	406
15	467

A plot of expected values from loglinear regression and from the nonlinear least-squares fit is:



The solid line is the fit from loglinear regression. The nonlinear fit (dashed line in the figure) does seem better for the higher counts but experience with a variety of population growth data suggests using the loglinear fit if, as is usually the case, one is mainly interested in studying rates of growth.

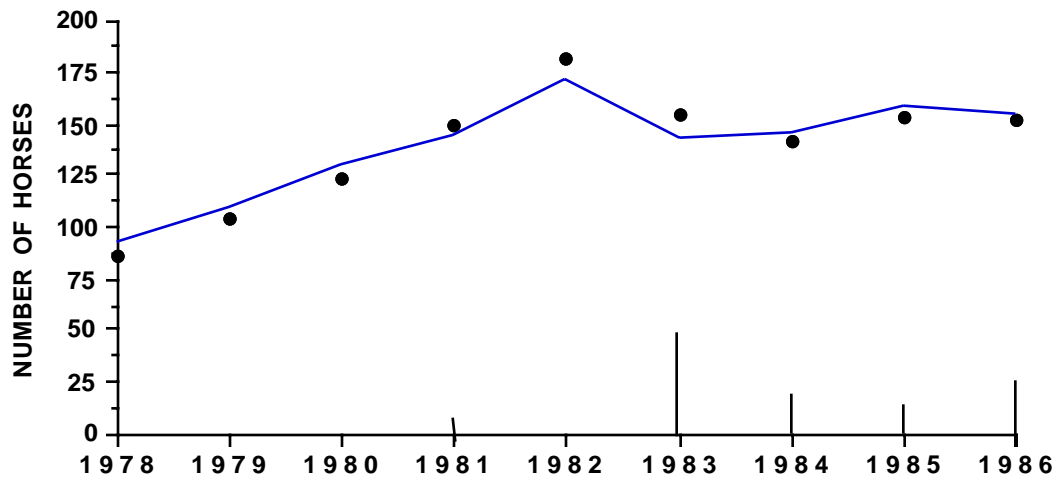
12.8.2 Use parametric regression bootstrapping (Ch. 2) to calculate approximate 95% confidence limits on the population growth rate obtained by loglinear regression in Exercise 12.8.1 and compare them with the limits obtained from the regression program in EXCEL.

12.8.3 Plot the rate of change for the logistic equation [Eqs.(12.12) and (12.26)] using the approximation given after eq.(12.26) which was used to make the plot of Fig. 12.3. This is a serious limitation for use of the logistic equation for the large vertebrates, as their rates of change do not seem to behave this way.

12.8.4 An alternative to the logistic is the “generalized logistic” used in eq. (12.35). Note that it was used with $z=1$ to approximate the ordinary logistic for Fig. 12.3. Repeat the plot of Fig. 12.3 (in EXCEL), and make companion plots with $z=2, 5$, and 11. Plot the rate of change and compare it with the rate of change obtained in Exercise 12.8.3. It is this nearly constant rate of change over much of the range of population growth that typifies the large vertebrates.

12.8.5 A set of data on feral horses (Garrott and Taylor 1990) is given below. Use Model I (Eqs. 12.22) and the ratio estimator of eq. (12.23) to estimate λ using EXCEL. Compare your results with the following plot.

YEAR	OBSERVED	REMOVALS
1978	86	0
1979	104	0
1980	123	0
1981	150	7
1982	181	0
1983	155	50
1984	142	20
1985	153	13
1986	152	27



Plot of feral horse data showing removals and fitted curve for Model I.

12.8.6 Using EXCEL and the constants given in Section 12.6 reproduce the results of Fig. 12.5 with eqs. (12.34) and (12.35). You can use this approach to reproduce many of the models given in the literature.